MAIZE INTROGRESSION INTO TEOSINTE— A REAPPRAISAL[1]

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ABSTRACT

Maize (*Zea mays* L. subsp. *mays*) and its wild relatives, the teosintes (*Zea* spp.) have been considered by many authors to be undergoing substantial reciprocal introgression. While there is evidence that some maize populations contain teosinte germplasm, the evidence for maize introgression into teosinte has been largely circumstantial. A re-consideration of the evidence for maize introgression into teosinte proved it wanting. Red sheath color, large grain size, triangular fruitcase shape, and the presence of internal chromosome knobs, all characters attributed to maize introgression into teosinte, appear rather to reflect the adaptation of particular teosinte populations to the exigencies of specific habitats. Apparently, the taxa of teosinte have remained relatively free of long-lasting maize contamination at least in respect to those characters that affect the survival of teosinte in the wild. Low-level introgression from maize to teosinte, although possible, remains undocumented.

Introgressive hybridization, or more simply, introgression, is the incorporation of genes from one population into another with a different adaptive norm (Anderson & Hubricht, 1938). This process is of obvious importance to taxonomists and evolutionists because, along with mutation, gene drift, and recombination, it is a potential source of evolutionary variation within and among species. Introgression is of particular interest to scientists studying cultigens and their wild ancestors because these plants generally lack barriers to hybridization and they often grow sympatrically. For these reasons, one would expect introgression between crop species and their ancestors to occur with some frequency.

The cultigen maize (*Zea mays* L. subsp. *mays*) and its wild relatives, the teosintes, have been considered model examples of reciprocal introgression (de Wet & Harlan, 1972; Heiser, 1973; Wilkes, 1977). The evidence for teosinte introgression into maize seems good. Where farmers in Mexico encourage the hybridization of teosinte and maize in an effort to "improve" their maize strains, the resultant maize populations have many teosintoid characteristics (Wilkes, 1970, 1977). The reverse introgression of maize germplasm into teosinte seems less likely to occur because maize has many characteristics that prevent it and its hybrids with teosinte from surviving in nature. Nevertheless, the frequency of maize-teosinte hybrids in the wild in Mexico and Guatemala (10% or more of the teosinte plants in a field may actually be hybrids), coupled with the fact that maize and teosinte show parallel variation over much of their range, has led some authors to conclude that many teosinte populations have been substantially altered by maize introgression. In this paper, I will review and reinterpret the evidence for maize introgression into teosinte and articulate the viewpoint that the teosintes have not been substantially altered by maize introgression.

A critical problem in the study of introgression is to distinguish natural evolutionary variation from that produced by introgressive hybridization (Anderson, 1953). This generally proves a difficult task because within any taxon there exists a certain amount of natural variation, some of which will inevitably be in the direction of other closely related taxa. For example, within many plant genera, one finds some natural variability for seed and fruit size. This being the situation, claims that those populations with intermediate-sized organs represent hybrids of the large and small organed forms should be viewed askance (cf. Weatherwax, 1918). Further, even if

a particular taxon demonstrates intermediacy for a number of morphological or genetic characters, thereby appearing to be of hybrid origin, this does not preclude the possibility that this taxon represents an evolutionary intermediate (cf. Mangelsdorf & Reeves, 1939: 207).

The introgression problem in *Zea* is particularly perplexing. Not only does cultivated maize commonly occur in the proximity of its wild relatives, but it has been observed to hybridize in the wild with all of them (Wilkes, 1967; Collins, 1921a; Iltis et al., 1979). In addition, there exists considerable variation in the shape and size of organs among the teosintes, which easily lends itself to the hypothesis that maize germplasm is introgressing into teosinte. The case for maize introgression into teosinte seems difficult to repudiate. Yet, one may interpret the variation in teosinte as natural evolutionary variation, and, as will be shown below, such an interpretation coincides well with known ecological and evolutionary principles.

In the following discussion, it is important that the reader have a basic knowledge of the taxonomic relationships in *Zea*. The genus is divided into two sections. Section *Luxuriantes* contains three species: (1) *Z. diploperennis* Iltis, Doebley & Guzman, a diploid perennial from Jalisco, Mexico; (2) *Z. perennis* (Hitchc.) Reeves & Mangelsdorf, a tetraploid perennial from Jalisco, Mexico; and (3) *Z. luxurians* (Durieu & Ascherson) Bird, an annual from southeastern Guatemala and Honduras. Section *Zea* contains a single species with three subspecies: (1) *Z. mays* subsp. *mays*, the cultigen; (2) *Z. mays* subsp. *mexicana* (Schrader) Iltis, a large spikeleted annual from high elevation of central and northern Mexico, including races Chalco, Nobogame, and Central Plateau; (3a) *Z. mays* subsp. *parviglumis* Iltis & Doebley var. *parviglumis* (Balsas teosinte), a small spikeleted annual from low or middle elevations in southwestern Mexico; and (3b) *Z. mays* subsp. *parviglumis* var. *huehuetenangensis* Iltis & Doebley, a genetically distinct form of this subspecies from western Guatemala (Iltis & Doebley, 1980; Doebley & Iltis, 1980; Doebley, 1983). As this taxonomy suggests, the teosintes of section *Luxuriantes* are not particularly closely related to the cultigen, whereas those of section *Zea* are so close as to be regarded as conspecific. Finally, in this discussion, I will, at times, mention the genus *Tripsacum* which, along with *Zea* forms the subtribe Tripsacinae of the tribe Andropogoneae of the family Gramineae.

HISTORICAL BACKGROUND

Since the time when Ascherson, Beadle, Collins, Kempton, Longley, and others first began to document the extent of variability among teosinte populations, researchers have demonstrated a bias in favor of maize introgression to explain this variability. Thus, Collins (1921a: 340, 345), who noticed that both maize and teosinte of the Valley of Mexico have dark red, densely pilose sheaths, speculated that teosinte acquired these characters from maize via introgression. Part of Collins's reason for proposing this explanation was that he had never before seen "pure teosinte" with these characters. Later, Mangelsdorf (1947: 165) and then Wilkes (1977) reiterated this idea.

Collins also (1921a: 350) theorized that perennial teosinte (*Zea perennis*) had hybridized with maize to produce annual teosinte. However, he offered no evidence to support this idea other than his observation that maize and teosinte show parallel variation wherever they co-occur. Collins apparently failed to recognize that such parallel variation could easily result from either teosinte introgression into maize or simply convergent evolution. A few years later, Collins (1925: 378, 1930: 201) modified his thesis somewhat by suggesting that either *Z. luxurians* (Florida type) or *Z. perennis* might have hybridized with maize to produce the Mexican annual teosintes (*Z. mays* subsp. *mexicana* and subsp. *parviglumis*). As evidence in support of this hypothesis, he reported that ". . . forms resembling the Mexican type [*Zea mays* subsp. *mexicana*] always appear in hybrids between Florida teosinte [*Zea luxurians*] and maize" (Collins, 1925: 378).

Kempton and Popenoe (1937: 216–217) discussed "the assumption of other workers" that the triangular shape of the fruitcase of Mexican annual teosinte represents the by-product of maize introgression into *Zea luxurians*, which has trapezoidal fruitcases. However, Kempton and Popenoe questioned the validity of this hypothesis based on their observation that the triangular "fruited" Huehuetenango teosinte occurs in "almost pure stands," and thus, is free of maize introgression. Ultimately, they decline to conclude, one way or the other, whether Mexican annual teosinte represents a good species or a hybrid of "pure teosinte" with maize (Kempton & Popenoe, 1937: 217).

Longley (1937, 1941a) proposed that the in-

ternal chromosome knobs (heterochromatic regions) of Mexican annual teosinte resulted from the contamination of "pure teosinte" (*Zea luxurians*), which has many terminal knobs, with maize, which is characterized by many internal knobs. However, he declined to rule out the possibility that the Mexican annual teosintes acquired their internal chromosome knobs via mutation, with *Z. luxurians* being their more primitive ancestor.

Mangelsdorf and Reeves (1938, 1939) went one step further than Collins, Kempton, and Longley and advanced their hypothesis that teosinte ". . . appears to be nothing more than *Zea* [the hypothetical wild maize] with a slight infection of *Tripsacum* germplasm" (1939: 209). This idea actually originated with Edgar Anderson (cf. Mangelsdorf & Reeves, 1939: 212; Anderson, 1969; Mangelsdorf, 1974: ix). Under the viewpoint of this hypothesis any variability in teosinte manifests nothing more than differences in the relative proportions of "wild maize" and *Tripsacum* germplasm (Mangelsdorf & Reeves, 1939: 215).

This view of variability in teosinte has influenced others as well. Thus, in his study of the genetic mechanisms controlling inheritance of inflorescence characters in maize-teosinte hybrids, Rogers (1950), a student of Mangelsdorf, found evidence that, in his view, called the purity of the Mexican annual teosintes into question. He reported that hybrids with Nobogame (*Zea mays* subsp. *mexicana*) produced the most maize-like inflorescences and those with southern Guatemalan teosinte (*Zea luxurians*) the least maize-like ones. Durango (*Z. mays* subsp. *mexicana*) and "northern" (western) Guatemalan (*Z. mays* var. *huehuetenangensis*) teosintes were intermediate in this regard. To Rogers, these results indicated that Nobogame teosinte is highly contaminated with maize, the other Mexican teosintes are somewhat less so, and southern Guatemalan teosinte is the least contaminated of all. He concluded that his evidence supports ". . . the hypothesis that the more maize-like teosintes represent the original teosinte with a substitution of maize germplasm on various chromosomes" (Rogers, 1950: 555).

Wilkes (1967), another of Mangelsdorf's students, considered the teosinte populations of Mexico and Guatemala to express various degrees of maize admixture. He believed teosinte in the Chalco region to be highly introgressed "as evidenced" by its dark red, hairy leaf sheaths, which are similar to those of the maize of this region (Wilkes, 1972: 1067–1077, 1977: 384–385). Wilkes (1967: 81), ostensibly disagreeing with Rogers (see above), found little evidence of maize introgression into teosinte in the Nobogame area. Wilkes (1967: 72) considered the principal direction of gene exchange in the Balsas river valley to be from teosinte to maize and not vice versa. Wilkes (1967: 82) reported hybrids to be rare in southeastern Guatemala, and thus, introgression unimportant. Wilkes (1967: 82) also concluded that teosinte in the Huehuetenango region of Guatemala was little introgressed by maize, though he found many hybrids of this teosinte and maize in the wild. Wilkes (1967: 80–81) considered the teosinte of the Mexican Central Plateau to show signs of maize admixture in its pistillate spike, including paired spikelets and a nonbrittle rachis. In addition, he regarded the large grain size and triangular fruitcase of some Central Plateau populations and of Chalco teosinte as evidence of maize introgression (Wilkes, 1977: 278). More recently, Wilkes (1979) proposed that all the racial varieties of annual teosinte resulted from the hybridization of maize with *Zea diploperennis,* coming full circle back to Collins's (1921a) similar suggestion involving *Zea perennis.*

Bird (1978: 362) also considered maize introgression to have played an important role in the morphology of extant teosinte populations. He regarded tall plants with large leaves, few tillers, a great number of and large fruitcases, and large caryopses as heavily introgressed by maize. Further, he hypothesized that Huehuetenango teosinte is a hybrid of maize and *Zea luxurians.*

Many authors have reiterated these contentions concerning the introgression of maize germplasm into teosinte (Heiser, 1973; Galinat, 1975; de Wet et al., 1978; de Wet & Harlan, 1972). However, a few authors have adjured this line of reasoning, and taken either the viewpoint that teosinte is not significantly introgressed by maize or that the evidence for such introgression is wanting (Melhus et al., 1949; Kato, 1976; Iltis & Doebley, 1980).

For many of the authors discussed above, their views on maize-teosinte introgression formed part of their models on the origin of corn because an understanding of teosinte is prerequisite to understanding the evolution of maize. As stated by Collins (1921b: 505) ". . . the many resemblances between maize and teosinte, together with the fact that the two forms interbreed with per-

fect freedom, make it certain that whatever the origin of maize it must be intimately associated with teosinte." Thus, in the early part of this century, when very little was known of teosinte, hybridization and introgression theories seemed to solve the dilemma of teosinte being genetically the same species as maize but morphologically too dissimilar from maize to be its ancestor.

RECONSIDERING VARIABILITY IN TEOSINTE

Five trends in teosinte variation lend themselves to easy interpretation as examples of maize introgression into teosinte. (1) *Grain size.* Because some teosinte populations produce larger grains than others, various authors (Wilkes, 1977; Bird, 1978) have either hypothesized or stated quite unequivocally that the large-grained forms show the effects of introgression from the relatively giant-grained maize. (2) *Fruitcase shape.* The fruitcases of the teosintes vary from trapezoidal through triangular but blunt on the axial side to triangular and pointed or "pinched" on the axial side. The pointed triangular forms, it has been argued, are the most introgressed and the trapezoidal the least (Kempton & Popenoe, 1937; Mangelsdorf & Reeves, 1939; Reeves, 1953; Wilkes, 1977). (3) *Sheath characters.* Teosinte in the Valley of Mexico, like the native maize of this area, possesses densely pilose and dark red leaf sheaths. Teosinte is said to have obtained these characters from maize through introgression (Collins, 1921a; Mangelsdorf, 1947; Wilkes, 1967, 1972, 1977). (4) *Disease resistance.* Teosinte from southeastern Guatemala expresses resistance to a common maize virus. According to one author it could have obtained this resistance from local races of maize, which are themselves resistant to the same disease (Brewbaker, 1979). (5) *Internal chromosome knobs.* Annual teosinte from southeastern Guatemala possesses only terminal chromosome knobs whereas the annuals of Mexico, as well as cultivated maize, have many internal knobs. As discussed above, Longley (1937, 1941a, 1941b) and others have suggested that the Mexican annual teosintes obtained their internal knobs from maize.

Despite the facility with which these assertions often have been made, there are other explanations that do not necessitate introgression. Phylogeny and ecology of teosinte populations furnish the basis for a more parsimonious explanation for variability in teosinte than ad-

mixture with maize. In the following discussion each of the aforementioned five trends is reconsidered in the light of this viewpoint.

Grain size. "The seed is one of the least plastic organs on a plant; plants respond to stress phenotypically by varying almost every other component of yield before seed size is affected" (Harper, 1977: 664). Seed size results from a delicate compromise between a great number of conflicting exigencies including available moisture, temperature, amount of competition, length of growing season, and many other factors (Harper et al., 1970; Stebbins, 1972; Harper, 1977). Once a species has optimally adapted its grain or seed size to local environmental conditions, it will vary the *numbers* produced 100-fold before varying *size* one-fold (Harper, 1977). Thus, one would expect natural selection against incorporation of maize germplasm in teosinte plants, which would upset the fragile adaptive balance they have obtained in relation to grain size. This ecological principle impels us to conclude that grain size is one of the least likely features of the teosinte plant to be altered by maize introgression.

In addition to the above theoretical reason for expecting little alteration in grain size because of maize introgression, there exists some empirical evidence to support such a view. This evidence lies in the mean cupulate fruitcase weights (including caryopsis) for the different taxa of teosinte. Quite simply, if maize introgression accounts for the variability in grain weight (size), then one would predict those taxa genetically closest to maize and crossing most frequently with it to have the largest fruitcases. The data, however, fail to meet this expectation in several ways. First, despite their greater genetic-evolutionary distance from maize, some species of *Tripsacum*, the perennial teosintes, and *Zea luxurians,* all produce much heavier fruitcases than *Zea mays* subsp. *parviglumis,* which is genetically more closely related to maize and crosses more frequently with it (Table 1) (Wilkes, 1977; Iltis & Doebley, 1980). Second, *Zea luxurians,* long recognized as one of the least maize-like teosintes and crossing but rarely with maize in its native habitat, produces grains often heavier than those of the supposedly greatly contaminated Chalco teosinte (*Z. mays* subsp. *mexicana*).

If not maize introgression, what then explains the observed variability in the grain or fruitcase size among the teosintes? There are several fac-

TABLE 1. Average weight (mg) of teosinte cupulate fruitcases with caryopsis (N = number weighed).

Species Population	Collection	Wt.	N
Tripsacum dactyloides, cult.			
Ft. Meade, Maryland		118	50
Zea diploperennis			
Manantlan, Jalisco	*Iltis et al. 1375*	75	100
La Ventana, Jalisco	*Guzman 777*	72	100
Las Joyas, Jalisco	*Iltis et al. 1250*	68	100
$\bar{x}$		72	
Zea perennis			
Los Depositos, Jalisco	*Iltis et al. 1050*	83	100
Zea luxurians			
Honduras	*Galinat 76-2076-B*	90	20
Ipala, Chiquimula	*Iltis G-42*	99	100
Agua Blanca, Jutiapa	*Iltis G-38*	86	100
El Progreso, Jutiapa	*Iltis G-5*	84	100
El Progreso, Jutiapa	*Iltis G-36*	76	100
$\bar{x}$		87	
Zea mays subsp. *mexicana*			
Churintzio, Michoacan	CIMMYT K69-3	62	100
Quinceo, Michoacan	*Iltis & Cochrane 276*	95	100
Los Reyes, Mexico	*Iltis & Lasseigne 769*	86	50
$\bar{x}$		87	
Nobogame, Chihuahua	*Gentry 17973*	58	30
Nobogame, Chihuahua	*Wilkes* (1967)	62	—
Zea mays subsp. *parviglumis*			
Balsas drainge:			
Huetamo, Michoacan	CIMMYT K67-15	50	50
Valle de Bravo, Mexico	CIMMYT K67-21	56	100
Tzitzio, Michoacan	*Iltis & Cochrane 308*	43	100
Palo Blanco, Guerrero	USDA 343237	31	100
SW Jalisco:			
La Huertita	*Guzman s.n.*	79	100
El Palmar	*Puga 11065*	73	100
Guatemala:			
San Antonio Huista	*Iltis & Lind G-120*	51	100
$\bar{x}$		53	

tors that seem to influence seed size in plants. First, the amount of *competition* that a species normally encounters influences the size of seeds produced. Species whose seedlings face intense competition require larger seeds than those of open habitats (Harper et al., 1970; Abrahamson & Gadgil, 1973; Carlquist, 1974; Werner & Platt, 1976). *Plant habit* also affects seed size, with perennials producing fewer and larger seeds than annuals (Salisbury, 1942; Hart, 1977; Primack, 1979). This results partly from the general occurrence of perennials in later seres (greater com-petition). *Length of growing season* influences seed size, with larger seeds being more easily formed in regions with long growing seasons (Baker, 1972). If other factors place a premium on small seed size in a region with a long growing season, then the plant will take advantage of the long growing season to produce a greater number of seeds rather than larger ones. *Available moisture* plays an important role in determining seed size, with small seeds common in wet areas and large seeds frequent in dry areas. Seedlings in drier habitats more frequently encounter drought
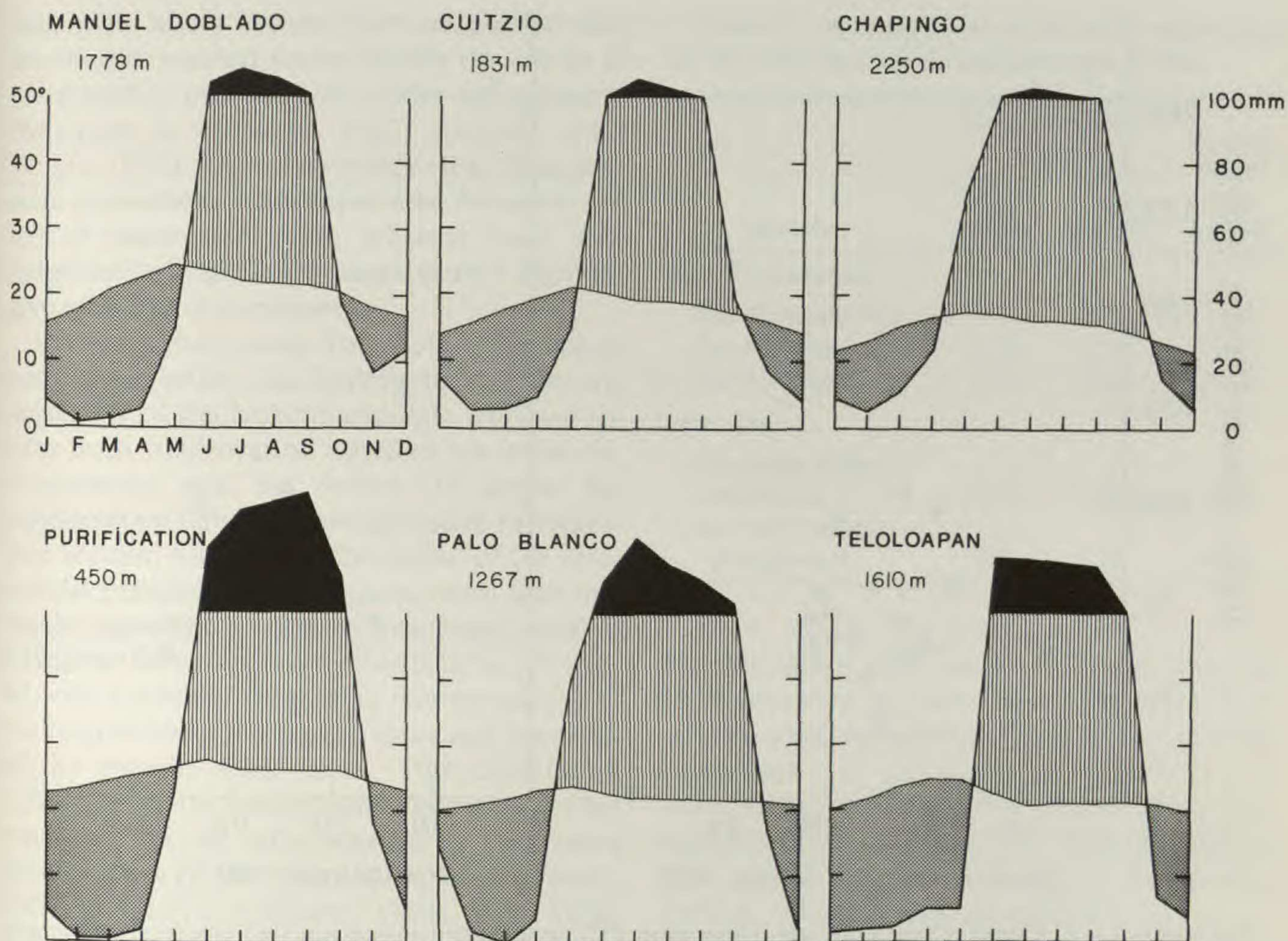
FIGURE 1. Climatic diagrams for some Mexican annual teosinte stations. The upper three diagrams represent sites of *Zea mays* subsp. *mexicana* and the lower three diagrams of subsp. *parviglumis*. On the diagrams the two curves represent mean monthly temperature (°C) and mean monthly precipitation (mm). Where precipitation exceeds 100 mm, curve is drawn at truncated scale (1 : 10) and the portion above 100 mm is black. Where rainfall curve exceeds temperature curve, space between curves is filled by vertical lines (or black, if rainfall exceeds 100 mm) whereas if rainfall curve falls below temperature curve, that space is filled by small dots. At top left of each diagram are name of station and altitude. These diagrams are patterned after those from the *Klimadiagramm-Weltatlas* (Walter et al., 1967) using data from Garcia (1974).

stress during the early stages of growth (Baker, 1972; Werner & Platt, 1976). Large seeds allow plants to establish themselves rapidly, and thus, reduce the likelihood of severe drought stress during early life. Further, larger seeds may germinate deeper in the soil where the moisture supply is more reliable (Schimpf, 1977).

Evidently, the ecological determination of seed size is immensely complex. Nevertheless, it is clear that seed size is an important aspect of the adaptive strategies of plants. Further, with so many factors influencing seed size and number, and with these factors often in competition with one another, it would be unreasonable to expect easy explanations for all the known variability in grain size among the teosintes. However, upon examining the fruitcase (including caryopsis) weights of these taxa (Table 1) the correspon-

dence of this information to environmental parameters seems good.

First, the perennial taxa produce relatively few large fruitcases as predicted. Both perennial taxa have fruitcases considerably larger than *Zea mays* subsp. *parviglumis*, and nearly as large as those of *Z. mays* subsp. *mexicana*. The large fruitcases of *Zea luxurians* could be explained by the relatively dry conditions under which this species grows with only 500–1,000 mm of rainfall annually, an environment similar in many ways to the Mexican Central Plateau. The difference between the small "seeded" populations of the Balsas river drainage (*Z. mays* subsp. *parviglumis*) and the larger "seeded" ones of the Central Plateau and the Valley of Mexico (*Z. mays* subsp. *mexicana*) appears to be closely related to available moisture. As shown by the climatic dia-
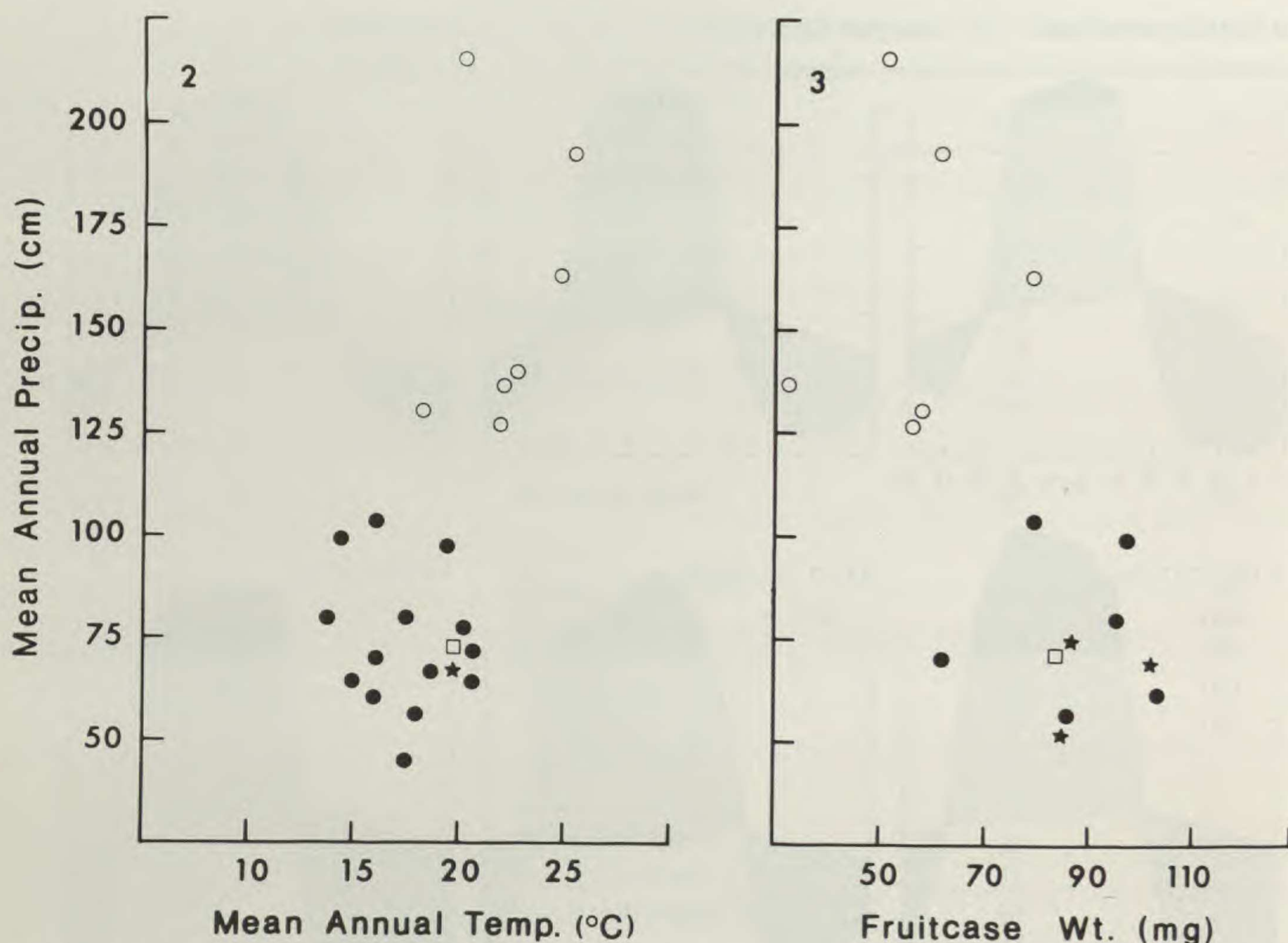
FIGURES 2–3.—2. A graph of mean annual temperature (°C) versus mean annual precipitation (cm) for various teosinte populations: *Zea perennis* (hollow square), *Zea luxurians* (stars), *Zea mays* subsp. *mexicana* (solid circles), and subsp. *parviglumis* (hollow circles). Data for Mexico from Garcia (1974) and that for Guatemala from Urrutia (1964).—3. Graph of mean annual precipitation against fruitcase weight demonstrating the negative correlation between these two variables; large fruitcases in dry areas and small ones in wet areas. Symbols as in Figure 2.

grams (Fig. 1), the Balsas sites receive a much greater amount of rain during the growing season than the Central Plateau and Valley of Mexico sites. The difference between the climates in the regions of *Zea mays* subsp. *mexicana* and subsp. *parviglumis* is dramatically portrayed in Figure 2, in which mean annual temperature is graphed against mean annual precipitation, while the relationship between fruitcase weight and precipitation is graphically displayed in Figure 3. The Huehuetenango population of *Z. mays* subsp. *parviglumis*, which occurs in a very wet area with 2,000–3,000 mm rainfall annually although with a longer growing season than Balsas teosinte, produces small fruitcases as well. Another point of interest in regard to the differentiation between the small and many-grained *Z. mays* subsp. *parviglumis* and the larger and fewer-grained *Z. mays* subsp. *mexicana* was noted by Wilkes (1967), namely that the grains of the later can successfully germinate deep (6 in.) in the soil while the former must germinate near the surface. This coincides well with Schimpf's (1977) observation that species from dry habitats produce large seeds capable of successfully germinating deep in the soil where the moisture supply is more reliable. Finally, that Nobogame teosinte produces grains of intermediate size despite its dry climate seems surprising but can be explained by the shortness of the growing season of this most northern of all teosintes, and by its adaptation to grow in thickets along streams (a locally and seasonally wet environment) (Wilkes, 1967, 1977).

In summary, an examination of the evidence suggests that for grain size and number the teosinte populations are highly variable, with each population adapted to the demands of its particular habitat and seasonal growth form.

Fruitcase shape.   The fruitcase in teosinte is composed of the female spikelet and its attached rachis segment. Its shape ranges from trapezoidal and *Tripsacum*-like through triangular though blunt on the axial side, and ultimately to triangular and sharply pointed, or "pinched," on the

axial side. Many authors have considered that the sharply pointed forms display the effects of *condensation* produced via maize introgression (Kempton & Popenoe, 1937; Reeves, 1953; Wilkes, 1977). According to this view, those teosinte populations with trapezoidal fruitcases are free of maize germplasm, whereas those with "pinched" triangular fruitcases show a high degree of maize contamination.

Using measurements from both male tassels and female spikes, the hypothesis that the triangularity of the teosinte cupulate fruitcase results from condensation acquired via maize introgression can be tested. If genes for condensation obtained through maize introgression account for the transformation of the trapezoidal fruitcases into triangular ones, then one would expect the procession from trapezoidal to triangular female rachis segments to be correlated with a gradual shortening (condensation) of the internodes of the central spike and branches of the teosinte male tassel. This expectation emerges from the demonstrated homology of the male and female inflorescences in *Zea mays* subsp. *mays* (Kellerman, 1895; Montgomery, 1906; Iltis, 1911; Anderson, 1944). From Table 2, one can readily see that no such correlation exists. Instead, those teosinte populations with trapezoidal fruitcases (sect. *Luxuriantes*) possess the shortest male internodes on both the central and lateral spikes, and those with triangular fruitcases (sect. *Zea*), the longest. Indeed, the triangular "fruited" teosintes do not have tassel internodes intermediate in length between those of the trapezoidal types and maize, but rather they have the longest tassel internodes (i.e., the least condensed) in all of *Zea*. These facts cast doubt on the claim that maize introgression into a teosinte with trapezoidal fruitcases gave rise to the teosintes with triangular fruitcases.

If maize introgression fails to explain the variation in teosinte fruitcase shape, what then can explain the diversity of observed forms? The answer might be quite simply that the triangular shape of the fruitcases of sect. *Zea* represents an evolutionary advancement over the more primitive trapezoidal shape found in sect. *Luxuriantes* and the genus *Tripsacum*. The triangular shape might allow more efficient packing of the rachis segments in the individual spikes or easier dispersal. If triangularity allows more efficient packing, then one might expect the ratio of the weight of the cupulate fruitcase to that of the caryopsis to be lower for the triangular type.

TABLE 2. A comparison of internode length (mm) for the male and female inflorescences of *Zea*.

Species	Male Internode Length		Female Fruitcase Length
	Central Spike	Lateral Branch	
Sect. *Luxuriantes*			
Zea diploperennis	3.16	3.06	7.30
Zea perennis	3.76	3.68	7.20
Zea luxurians	4.39	4.48	8.33
Sect. *Zea*			
Zea mays subsp. mexicana	5.13	5.65	6.92
Zea mays subsp. parviglumis	5.54	5.96	6.05

Measurements made on the fruitcases show this to be generally the case with a progression from large to small ratios from *Tripsacum* > *Zea diploperennis* > *Z. perennis* > *Z. luxurians* > *Z. mays* subsp. *mexicana* > *Z. mays* subsp. *parviglumis* (Table 3). However, there is considerable overlap between *Z. luxurians* and *Z. mays* subspp. *mexicana* and *parviglumis*.

In summary, the observations (1) that there is no clear-cut correlation between condensation in the male and female teosinte inflorescences to support the maize introgression hypothesis, and (2) that fruitcase shape may reflect different degrees of divergence from the primitive trapezoidal *Tripsacum*-like condition to a more efficient triangular shape, undermine the interpretation that variation in fruitcase shape is evidence for maize introgression into teosinte.

Sheath color and pilosity. Introgression has also been enlisted to explain the co-occurrence of dark red coloration and extreme pilosity on the leaf sheaths of maize and teosinte in the Valley of Mexico (Collins, 1921a; Mangelsdorf, 1947; Wilkes, 1967, 1972). Wilkes hypothesized that these teosintes are maize mimics (which evolved as a result of inadvertent selection) that copy the coloration of the native maize of the region and thus are able to escape the eye and sickle of the *campesinos* weeding their corn fields. Wilkes (1972, 1977) like his predecessors, Collins and Mangelsdorf, evoked maize introgression as the mechanism by which the teosintes of the Valley of Mexico acquired the genes for this "protective" coloration, although he did not dismiss convergence as an alternative hypothesis. Initially, one might ask, could not introgression have

TABLE 3.   Mean weight of the total fruitcase and caryopsis, and the ratio of these two values for some teosintes and *Tripsacum* (N = number weighed).

Species Population	Collection	Total Fruitcase Wt. (mg)	Caryopsis Wt. (mg)	Ratio	N
Tripsacum dactyloides					
Ft. Meade, Maryland		122	35	3.69	10
Zea diploperennis					
Las Joyas	*Iltis et al. 1250*	75	25	2.98	10
Manantlan	*Iltis et al. 1375*	75	25	2.97	10
x̄				2.98	
Zea perennis					
Los Depositos	*Iltis et al. 550*	106	36	2.92	10
Zea luxurians					
Agua Blanca	*Iltis G-38*	87	31	2.78	10
Ipala	*Iltis G-42*	125	38	3.05	12
Progreso	*Iltis G-36*	87	37	2.35	16
Progreso	*Iltis G-5*	90	37	2.40	12
x̄				2.65	
Zea mays subsp. *mexicana*					
Quinceo	*Iltis & Cochrane 276*	109	44	2.48	12
Los Reyes	*Iltis & Lasseigne 769*	85	36	2.36	10
Amecameca	*Iltis & Cochrane 176*	97	44	2.18	10
Chalco	*Iltis & Cochrane 175*	103	43	2.38	10
x̄				2.35	
Zea mays subsp. *parviglumis*					
Tzitzio	*Iltis & Cochrane 308*	45	23	2.04	10
San Antonio Huista	*Iltis & Lind G-120*	54	23	2.45	15
La Huertita	*Guzman s.n.,* cult.	82	38	2.17	10
x̄				2.22	

proceeded in the opposite direction from teosinte into maize? Unfortunately, this possibility has received little consideration.

In order to explore other potential explanations for the occurrence of dark red pilose sheaths in teosinte and maize from the Valley of Mexico, I will first review the functions these traits might fulfill in maize and teosinte. Red tissue coloration results from the presence of anthocyanins, which fulfill many different functions for the species which produce them (McClure, 1975; Harborne, 1976). One particular function, cold resistance, has been attributed to anthocyanins that occur as a more or less permanent part of leaf tissues. Speculation that anthocyanins help adapt plants to cold environments first emerged when botanists began to notice that species of the cold high altitudes are often more deeply red pigmented than similar species at warmer lower elevations (Kerner, 1891; Bonnier, 1895; Clau-

sen et al., 1940). Researchers have also noted that plants develop greater red coloration when artificially grown in cold environments. This is true for *Hydrocharis* (Overton, 1899), *Impatiens* (Alston, 1959), *Pyrus* (Creasy, 1968), *Chrysanthemum* (Rutland, 1968), and *Euphorbia* (Marousky, 1968). More recently Ganders et al. (1979) noted that in populations of *Collinsia, Mimulus,* and *Trifolium,* phenotypes with dark red spotted leaves are more frequent in colder microhabitats. These latter authors hypothesized that the dark red pigmentation in the leaves of these species functions to absorb radiant energy, and thus, warm the plant. Galinat (1967) proposed this same hypothesis, viz. that red pigmentation acts to absorb radiant energy, thereby warming the plant, to explain the predominance of red plant color among high altitude varieties of maize in Latin America. Galinat noted the lack of experimental verification for this hypothesis. Since that

TABLE 4. Sheath pubescence[a] and color,[b] altitude (m)[c] and mean annual temperature (°C)[c] for some teosinte populations.

Species Population	Collection	Sheath Pubescence	Sheath Color	Mean Annual Temp.	Alt.
Zea mays subsp. *mexicana*					
Valley of Mexico:					
Amecameca	USDA 343246	3	2	14.4	2,425
Chalco	*Iltis & Doebley 401*	3	2	15.9	2,250
Los Reyes	*Iltis & Lasseigne 769*	3	2	16.0	2,180
Central Plateau:					
Patambicho	*G. Prior s.n.*	2	2	16.4	2,132
Quinceo	*Iltis & Cochrane 276*	2	2	17.6	1,940
Churintzio	CIMMYT K 69-3	1	1.5	—	1,900
Nobogame	ex G. Beadle	1	1.5	—	1,850
Degollado	*Puga 11066*	1	1	—	1,625
Zea mays subsp. *parviglumis*					
Balsas drainage:					
Valle de Bravo	CIMMYT K 67-21	0	1	18.3	1,350
Teloloapan	CIMMYT W 71-3	0	1	21.9	1,610
Palo Blanco	USDA 343237	0	0	22.0	1,267
Jalisco:					
El Palmar	*Puga 11065*	0	0	—	980
La Huertita	*Guzman s.n.*	0	0	—	1,100
Jirosto	*Iltis & Nee 1480*	0	0	—	500
Purificacion	*Iltis & Nee 1471*	—	—	25.4	450
Guatemala:					
San Antonio Huista	*Iltis & Lind G-120*	0	0	20.0	1,300

[a] 0 = essentially glabrous; 1 = hairy along upper sheath margins; 2 = pubescent throughout; 3 = densely pubescent throughout.
[b] 0 = green or slightly red; 1 = red; 2 = dark red.
[c] This information from Garcia (1974) and Urrutia (1964).

time, however, two studies have shown that varieties of maize with dark red sheaths stay warmer than similar dilute red types (Greenblatt, 1968; Chong & Brawn, 1969).

If anthocyanins do aid in warming the teosinte plant as experimentation shows they do in maize, then one would predict that those teosinte populations growing in the coldest environments would be the most heavily pigmented and those in the warmest areas the least pigmented. While looking for characters to distinguish various teosinte populations, I took some notes on the degree of coloration of the sheaths among 14 populations I had growing in Florida. Each population was grown in two different randomly assigned rows. Without knowing the origin of the plants in a row, I subjectively categorized the sheaths of the plants in it as either green or slightly red (0), red (1), or dark red (2) (see Table 4). A two-sided Tau-test (a non-parametric test of associ-

ation) shows significant correlations of both mean annual temperature ($P < 0.02$) and altitude ($P < 0.01$) (which in Mexico is closely related to temperature) to sheath color (Table 4). This suggests that teosinte populations display varying degrees of red coloration not as the result of fortuitous hybridizations with maize or even as an attempt to mimic maize (though red coloration might certainly function in that capacity and thus be reinforced), but rather as an adaptation to a local environmental condition—temperature.

The situation with sheath pubescences is similar to that with anthocyanins. Again, naturalists and ecologists have often noted that dense pubescence functions to preserve the warmth within plants in cold environments (Daubenmire, 1947: 186; Carlquist, 1974: 563–565). Dense pubescence increases the boundary layer surrounding the organ it bedecks, thus causing temperature fluctuations in the plant to lag behind those

of the environment. In this way the plants may escape injury during short periods of extreme temperature (Daubenmire, 1947: 172). Various naturalists have commented on the correlation between the density of pubescence and temperature in *Potentilla* (Clausen et al., 1940: 141–142) and *Senecio* (Carlquist, 1974: 563–565).

Returning to Table 4, it is clear that there exists in teosinte a correlation between temperature and density of pubescence, with the most hirsute populations found in the highest coldest habitats and the glabrous ones in the lower warmer sites. A two-sided Tau-test of association shows significant correlations of both mean annual temperature ($P < 0.01$) and altitude ($P < 0.01$) to the density of sheath pubescence. As with sheath coloration these data suggest that pubescence in teosinte results not from haphazard hybridizations with maize, but from each individual population adapting to the exigencies of its particular habitat.

Although coloration and pubescence in teosinte have their adaptive functions, this does not *preclude* the possibility that teosinte obtained these characters from maize. However, teosinte is a natural wild plant that has undoubtedly persisted in the diverse climatic regions of Meso-America for tens-of-thousands of years. There can be little doubt that it achieved its present adaptation long before man and maize arrived on the scene.

A final curious fact worthy of comment concerns the manner in which both maize and teosinte of the Valley of Mexico carefully restrict the intense expression of dark red pigmentation and dense pilosity to the leaf sheath, thus leaving the photosynthetic leaf blade essentially free of all hairs and red color. This, too, bespeaks the adaptive importance of the traits. The function of the leaf sheath is primarily protective rather than photosynthetic, its salient role being to shield the stem from both insects and desiccation. In this same manner, the red color and hairiness of the sheaths of certain teosintes might act to maintain the temperature of the stem at a slightly higher temperature than otherwise possible especially late in the growing season when nights are cool.

In summary, given (1) that one likely role of anthocyanaceous pigmentation and dense pubescence is to protect plants in cold environments, (2) that maize and teosinte are C-4 plants, and thus, thermophiles, and (3) that there is a close correlation between both degree of red col-

oration and pubescence on the one hand, and mean annual temperature on the other, it is highly unlikely that teosinte acquired these characters by sporadic hybridization with maize. Further, there is no better reason for presuming that dark red coloration and dense pubescence would have introgressed from maize to teosinte than there is for expecting the reverse introgression from teosinte to maize. In fact, given that teosinte is a highly successful wild species and that maize is not, the latter seems much more probable.

Disease resistance. Brewbaker (1979) suggested that *Zea luxurians* obtained resistance to Maize Mosaic Virus and the rust, *Puccinia sorghi,* when genes for resistance to these diseases were transferred to it from local Caribbean maizes. However, introgression, if it occurred at all, probably moved in the opposite direction—from teosinte into maize. The reasons for this are quite simple. First, *Zea luxurians* is the most primitive annual species in *Zea,* and thus, closely related to the perennials *Z. perennis* and *Z. diploperennis* (Doebley & Iltis, 1980). These, and most perennials, of necessity, maintain high disease and insect resistance because their sedentary and long-lived life-style renders them easily locatable by pests, which they tend to accumulate (Nault & Delong, 1980; Nault et al., 1980). Annuals, however, which do not accumulate pests or disease because of their annual habit, generally show less resistance to disease and predation (Feeny, 1976). Thus, it appears likely that *Zea luxurians,* which resembles the perennials morphologically, cytologically, and genetically (cf. Doebley & Iltis, 1980), retains, as a legacy of its phyletic affiliation with the primitive perennial taxa of *Zea,* a low susceptibility to disease.

Chromosome knobs. Longley and others have argued that the internal chromosome knobs of the teosintes in Mexico came from maize, and that the original "pure teosinte" (*Zea luxurians*) possessed only terminal knobs. On the surface of it, this suggestion seems fairly improbable, for if the Mexican teosintes are merely *Zea luxurians* with a "slight infection" of maize germplasm, then one would expect them to have chromosome knob patterns more closely resembling the pattern of *Zea luxurians* than they do. Rather, the Mexican teosintes have knob patterns essentially identical to maize (i.e., they have many internal knobs). The similarity between the Mexican teosintes and maize would seem best explained not by introgression, but by considering these teosintes as ancestral to maize (Kato, 1976).

Other available evidence also lends little credence to the thesis that knobs introgress from maize into teosinte. Kato and Galinat (1975), in a study of the occurrence of chromosome knobs among sympatric populations of maize and teosinte in the Chalco and Balsas regions, found no clear-cut documentation for introgression in either direction. And, as Kato (1976) demonstrated, the annual teosintes of Mexico possess some knob positions that are found neither in maize nor in *Zea luxurians*. The hypothesis that the Mexican annual teosintes are a mixture of maize and *Z. luxurians* does not account for the presence of these knob positions unique to the Mexican annual teosintes. If these Mexican annuals, like other teosintes, are the products of gradual evolutionary development from a common ancestor, however, then the unique knob positions of these teosintes, like their distinguishing morphological features, would have had sufficient time to arise in response to varying environments (Kato, 1976).

CONCLUSION

References to maize introgression into teosinte are numerous in the literature on teosinte. As shown above, the evidence for such introgression is largely circumstantial, and this evidence may be more plausibly interpreted as the result of adaptive radiation. Why then have researchers displayed such a bias in favor of the introgression hypothesis? There is one primary reason. Authors who believed that maize evolved from an unknown wild maize sought an explanation for teosinte that could remove it as a possible ancestor of maize. Thus, they interpreted the various forms of teosinte as nothing more than *Tripsacum* or a primeval teosinte with varying degrees of maize germplasm.

All things considered, there appears to be little or no clear-cut evidence to support the idea that the teosintes have been greatly altered by maize introgression. Whether one considers grain size, fruitcase shape, sheath color and pilosity, chromosome knob positions, or disease resistance, the patterns of variation among the populations of teosinte can best be explained on the basis of ecology and phylogeny. Seen from the viewpoint of the ecologist and evolutionist, *Zea* is not a helter-skelter conglomeration of maize-*Tripsacum* or maize-*Zea luxurians* hybrids, but rather an orderly product of allopatric variation among local populations that strikingly displays the effects of natural selection and geographic speciation.

Finally, the goal here has not been to take the undoubtedly indefensible position that never in the history of maize-teosinte sympatry has a single gene crossed the bridge from maize to teosinte, but rather that at present, only circumstantial evidence of such crossings can be found, and further, that such introgression holds little hope of permanently affecting characters essential to the survival of the teosinte plant in the wild. For these reasons, I believe that the morphology and general character of the teosinte populations as we perceive them today are in all likelihood not substantially altered from the condition in which they existed prior to the domestication and dispersal of maize.

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